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Human impacts on global freshwater fish biodiversity

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Abstract :

Freshwater fish represent one-fourth of the world's vertebrates and provide irreplaceable goods and services but are increasingly affected by human activities. A new index, Cumulative Change in Biodiversity Facets, revealed marked changes in biodiversity in >50% of the world's rivers covering >40% of the world's continental surface and >37% of the world's river length, whereas <14% of the world's surface and river length remain least impacted. Present-day rivers are more similar to each other and have more fish species with more diverse morphologies and longer evolutionary legacies. In temperate rivers, where the impact has been greatest, biodiversity changes were primarily due to river fragmentation and introduction of non-native species.

Main Text:

Rivers and lakes cover less than 1% of the Earth's surface but they host large levels of biodiversity, including near 18,000 fish species that represent one quarter of global vertebrates (*1-3*). These freshwater fishes support the functioning and stability of ecosystems through their contribution to biomass production and regulation of trophic networks and nutrient cycles (*4*). Freshwater fishes also contribute to human welfare as key food resources (*5*), and for recreative and cultural activities (*2*, *6*).

For centuries human populations have directly affected fish biodiversity (*7*) through extraction and introduction of non-native species (*8*, *9*). Human activities have also modified the natural environment by changing land uses, altering flow regimes, fragmenting rivers by dams, polluting soil and waters and altering climate, actions that indirectly favor extinction of native species and/or establishment of non-native species (*10-13*). Consequently, these direct and indirect anthropogenic impacts have led to modification of local species compositions (*8*, *9*). However, biodiversity is not restricted to purely taxonomic components but also includes functional and phylogenetic diversities. These two latter facets determine how organisms affect ecosystem functioning and stability (*14-18*) and are thus essential for conservation.

Here, we assess the extent to which six key facets of freshwater fish biodiversity (taxonomic, functional and phylogenetic richness and corresponding dissimilarities between river basins) have changed over the last two centuries in 2,456 river basins, covering almost the entire continental surface of the Earth (excluding deserts and poles) and hosting >14,000 species (>

80% of the global freshwater fish pool) (*19*). We computed an index of cumulative change in biodiversity facets (CCBF) which ranges from 0 to 12 with higher scores depicting stronger changes across more biodiversity facets. A score higher than 6 indicates either changes in all the six facets, or changes higher than median in more than three biodiversity facets (Fig. 1) (*20*). We further unravel the natural and anthropogenic drivers that have led to the observed changes across the main regions of the world.

More than half of the river basins (52.8%, 1,297 rivers covering 40.2% of the world continental surface and 37.3% of the world river length) show CCBF scores higher than 6 (Fig. 2), revealing deep and spatially distributed anthropogenic impacts on fish biodiversity. In contrast, one third of the river basins (35.7%, 878 rivers) did not experience changes in local richness but only changes in dissimilarity with assemblages from the same realm (Fig. S1). Those least impacted river basins are mostly small-sized and occupy only 13.4% of the world river basin surface and support 3,876 species, only 21.7% of the world fish fauna. Moreover, the least impacted rivers are overrepresented in Afrotropical and Australian regions, whereas the Neotropics, although being the richest in species, functional and phylogenetic diversity (*21*, *22*) account for less than 6% of the "least impacted" category (Fig. S1).

Fish assemblages from the temperate regions of Nearctic, Palearctic and Australian realms experienced the largest biodiversity changes, with more than 60% of the rivers reaching a CCBF score higher than 6 (Fig. 2 a,b). Overall biodiversity changes in temperate regions (CCBF = 8.6 ± 0.1, mean ± standard error) were higher than in tropical rivers (CCBF = 5.1 ± 0.1). For instance, large temperate rivers such as the Mississippi, Danube, or Murray-Darling show

CCBF scores higher than 8, whereas large tropical rivers, such as the Amazon, Congo or Mekong were less impacted (CCBF = 6, Fig. S2). Such a spatial pattern is consistent with previous studies on changes in taxonomic richness and dissimilarity of freshwater fishes (*8, 9*), and with historical reports on anthropogenic degradation of ecosystems (*23*), but contrasts with changes observed in other taxa for which changes in biodiversity were the highest in tropical regions [e.g., for marine biome (*24*), forest (*25*)].

Mapping the patterns of changes across the six diversity components revealed discrepancies between richness facets (Fig. 3). Except for a few rivers in the northern part of the Palearctic and Nearctic realms, fish biodiversity did not decline in most of the rivers (Fig. 3 a,b,c). This markedly differs from recent results documenting the decline in freshwater living resources at the local scale (i.e. over 1-10 km of river stretch) within some of these river basins (*12, 26*). Interestingly, we report an inverse trend in freshwater fish for local taxonomic, functional and phylogenetic richness in more than half of the world rivers (Fig. 3 a,b,c, Fig. 4). This increase in local diversity is primarily explained by anthropogenic species introductions that compensate for or even exceed extinctions in most rivers (*27*). 170 fish species went extinct in a river basin but this number might be underestimated due to time lag between effective extinction and published extinction reports (*28*). In addition, 23% of freshwater fish species are currently considered as threatened (*29*), which might turn to increase extinctions in the near future (*26*).

In addition to the overall increase in richness of fish assemblages in river basins, a general declining trend in biological dissimilarity between river basins, that is biotic homogenization, appears pervasive throughout the world's rivers (Fig. 3 d,e,f). Functional dissimilarity was the most impacted facet with a decrease in 84.6% of the rivers while taxonomic dissimilarity and phylogenic dissimilarity decreased in only 58% and 35% of the rivers (Fig. 3 d,e,f). The discrepancy between change in functional diversity and changes in taxonomic and phylogenetic diversity (Fig. 4) primarily stems from the origin of non-native species introduced in rivers. Species translocated from a river to nearby basins promote losses of dissimilarity because they often already occur as natives in many rivers of the realm and are often functionally and phylogenetically close to other native species (9, *30*). In contrast, exotic species (i.e. originating from other realms) are less frequently introduced and their divergent evolutionary history with native species led to increase phylogenetic dissimilarity of their recipient rivers (*30*). For instance, the exotic species introduced in only a few rivers of Europe (e.g., the mosquitofish, *Gambusia affinis*, established in south-western Europe or the brook trout, *Salvelinus fontinalis*, established in cold-water ecosystems) (*30*), markedly enhanced the phylogenetic dissimilarity between those rivers. However, exotic species even from distinct evolutionary lineages could share functional traits with some native species, hence leading to increase phylogenetic dissimilarity but decrease functional dissimilarity (Fig. 3). For instance, European trout, *Salmo trutta* and Pacific Salmon, *Oncorhynchus mykiss*, belong to an order (Salmoniformes) absent from the Australian realm but those exotic salmonids are functionally similar to some native Australian fishes such as the spotted mountain trout, *Galaxias truttaceus* (Osmeriformes) (*31*).

The CCBF score was positively linked to human activities related to the industrialization and economic development, such as human footprint [FPT, (*23*)], with an increase of biodiversity changes with the FPT in all the industrialized and populated realms. River fragmentation by dams, represented by the degree of fragmentation index [DOF, (*32*)], was also a widespread disturbance in the Nearctic and Palearctic realms (Fig. 2c) that experienced intensive damming for more than a century (*33*). Fragmentation by dams was also a significant driver of biodiversity change in the Neotropics, probably due to the rise of hydropower dam construction in this realm (*34*). Higher DOF values were reached in small or medium sized rivers, whereas the largest and most diverse rivers such as the Amazon, Orinoco or Congo remain mostly free flowing (*32*), but the current rise of dam construction on those rivers (*35, 36*) will constitute a major threat to their biodiversity. Apart from river fragmentation, consumptive water use for agriculture and industry [USE, (*32*)] was a significant driver of CCBF increase in the Nearctic realm, where water withdrawal for agriculture is intense (*32, 37*) and act in synergy with increasing DOF. In the Afrotropics, USE was the only significant human driver of CCBF, due to marked consumptive water use in regions with marked seasonal aridity (*32*, *37*). In addition, the CCBF score was positively correlated to the richness in native species in most of the realms, indicating that the most speciose rivers are also the most impacted by biodiversity changes. Moreover, no negative associations between the species richness and the CCBF were observed, providing little support to the hypothesis of biotic resistance that assumes a higher resistance of species-rich assemblages against disturbances (*38-40*).

Conserving freshwater fish diversity in the least impacted rivers (accounting for 13.4 % of the world basin surface) will remain under the target to protect at least 30% of the Earth's surface by 2030, proposed by a broad coalition of environmental organizations (*41, 42*). This result suggests that reaching the freshwater fish target must involve consideration of not only the least impacted rivers, but also areas where biodiversity has already been eroded by human activities. Moreover, conservation has moved toward systematically identifying regions in need of protection (*43*). The discrepancy in biodiversity erosion we report between freshwater and marine and terrestrial ecosystems (*24*, *25*) demonstrates that current measures of biodiversity erosion, derived from marine and terrestrial organisms, do not apply to freshwaters, and thus underlines the need to develop freshwater-focused conservation priorities. In addition, the mismatches between changes in taxonomic, functional and phylogenetic dissimilarities among the world freshwater fish fauna highlight the risk of evaluation based on change in a single facet as a surrogate of the changes in other facets. More importantly, our results highlight the need to consider the cumulative and synergistic effects of multiple human activities on the complementary facets of biodiversity. The CCBF index we propose presents a holistic measure of multiple measures of biodiversity change and offers potential for prioritizing and informing adaptive management and global conservation targets. Future studies and planning need to expand the focus from simple loss of species to integrated changes in facets of biodiversity resulting from interactions between synergetic human activities.

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Supplementary Materials:

Materials and Methods

Figs. S1-S4

Table S1

References (44-81)

Table S2 (separate file)

Table S3 (separate file)

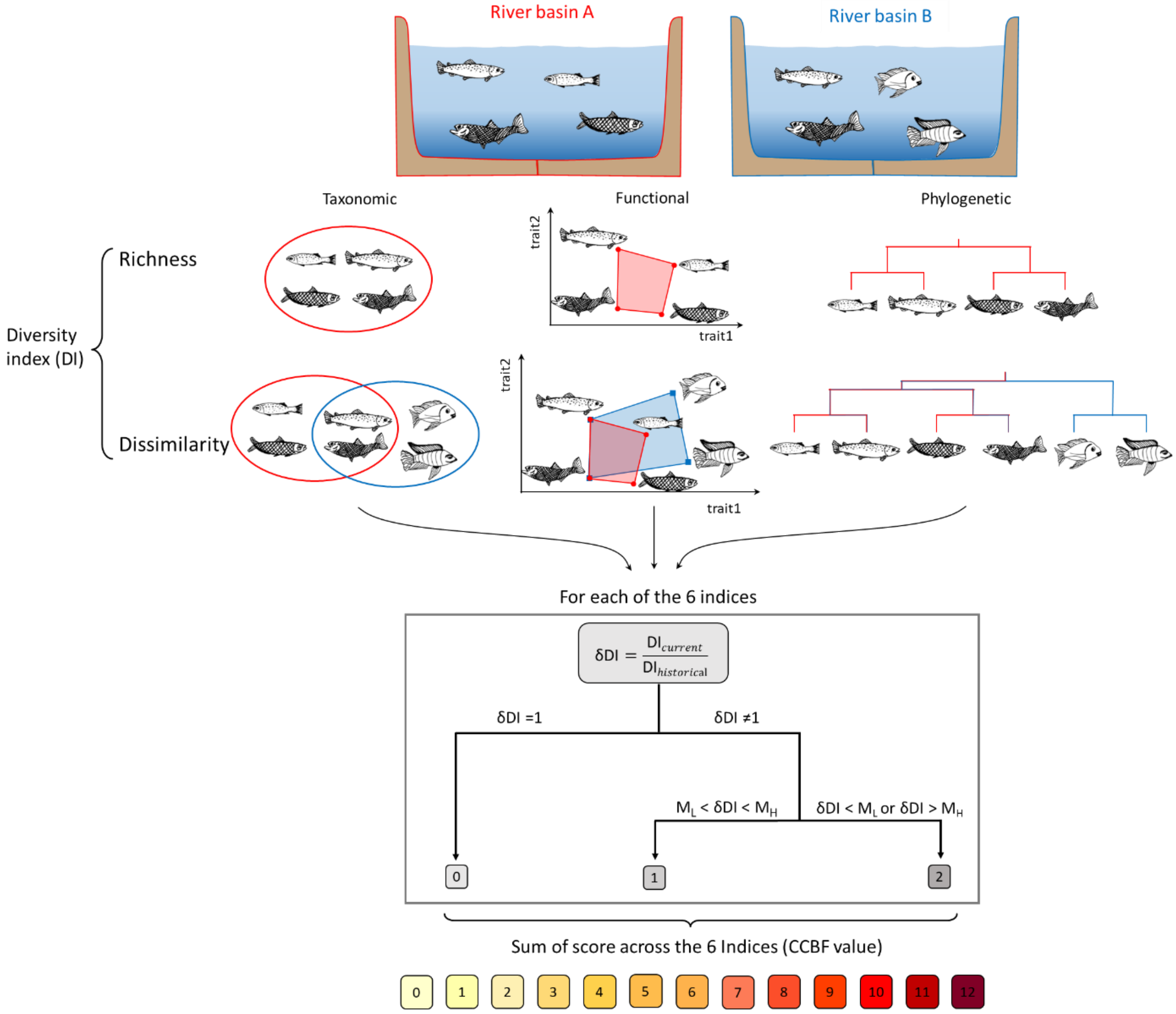


Fig. 1. Framework to measure the cumulative change in biodiversity facets (CCBF). δDI represents the change of a single diversity index among the six considered (Taxonomic richness, Functional richness, and Phylogenetic richness within each river basin and Taxonomic dissimilarity, Functional dissimilarity and Phylogenetic dissimilarity between pairs of basins); M_L is the median of all the values lower than 1, M_H is the median of all the values higher than 1. Score is used to compute the CCBF index.

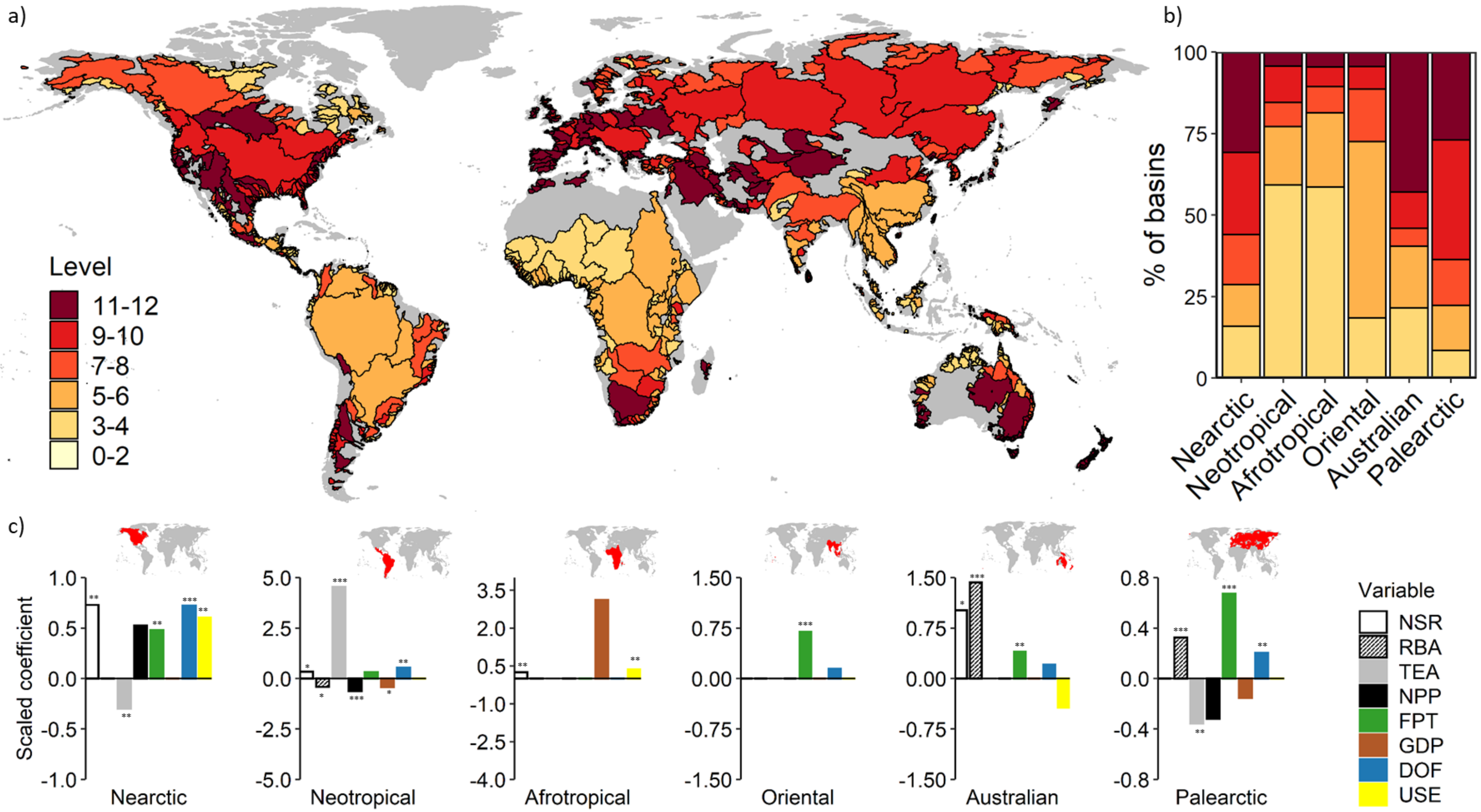
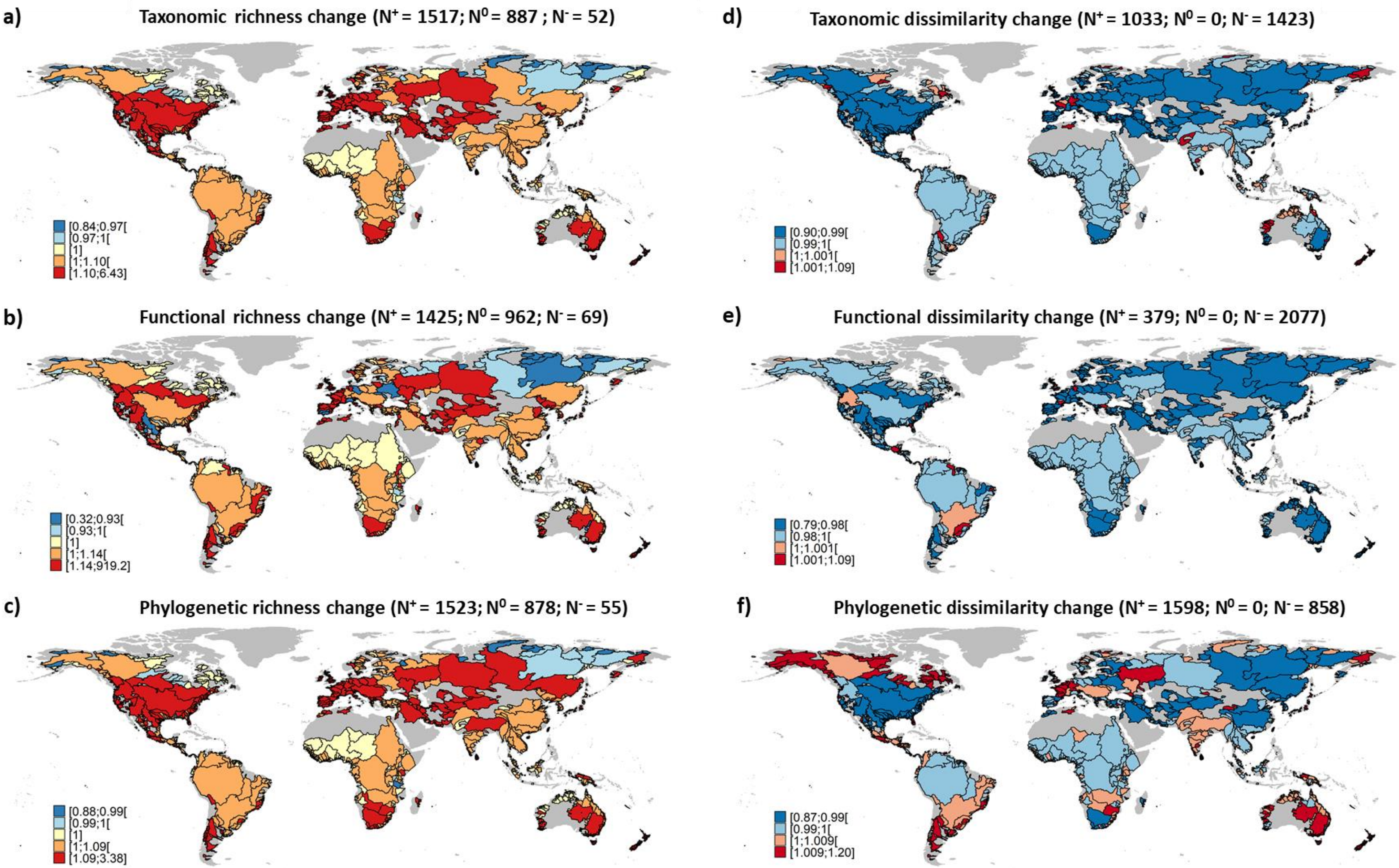


Fig. 2. Cumulative change in biodiversity of freshwater fish faunas. Cumulative index accounts for the sum of the changes in the six diversity indices: three facets (taxonomic, functional and phylogenetic) measured at two scales (local and regional). **a)** Map of the changes in 2,456 river

basins; **b)** percentage of river basins for six intensities of change in each biogeographic realm; **c)** scaled coefficient of the eight drivers of biodiversity change in autoregressive error model in each realm. (NSR: native species richness; RBA: river basin area; TEA: temperature anomaly since the last glacial maximum; NPP: net primary productivity; FPT: human footprint; GDP: gross domestic product; DOF: degree of fragmentation; USE: consumptive water use). Number of river basins used in the models: Afrotropical, n=198; Australian, n=525; Nearctic, n=241; Neotropical, n=350; Oriental, n=292; Palearctic, n=729. (*** $P < 0.001$; ** $P < 0.01$; * $P < 0.05$)



a)
Taxonomic richness change (N^+ = 1517; N^0 = 887 ; N^- = 52)
[0.84;0.97[
[0.97;1[
[1]
[1;1.10[
[1.10;6.43]
b)
Functional richness change (N^+ = 1425; N^0 = 962; N^- = 69)
[0.32;0.93[
[0.93;1[
[1]
[1;1.14[
[1.14;919.2]
c)
Phylogenetic richness change (N^+ = 1523; N^0 = 878; N^- = 55)
[0.88;0.99[
[0.99;1[
[1]
[1;1.09[
[1.09;3.38]
d)
Taxonomic dissimilarity change (N^+ = 1033; N^0 = 0; N^- = 1423)
[0.90;0.99[
[0.99;1[
[1;1.001[
[1.001;1.09]
e)
Functional dissimilarity change (N^+ = 379; N^0 = 0; N^- = 2077)
[0.79;0.98[
[0.98;1[
[1;1.001[
[1.001;1.09]
f)
Phylogenetic dissimilarity change (N^+ = 1598; N^0 = 0; N^- = 858)
[0.87;0.99[
[0.99;1[
[1;1.009[
[1.009;1.20]

Fig. 3. Changes in each of the six biodiversity indices for the world freshwater fish assemblages (2,456 river basins). **a)** Taxonomic richness change; **b)** Functional richness change; **c)** Phylogenetic richness change; **d)** Taxonomic dissimilarity change; **e)** Functional dissimilarity change; **f)** Phylogenetic dissimilarity change. Legend values are the original ratio $DI_{current}/DI_{historical}$. Number of basins where fish diversity increased (N^+), remained unchanged (N^0) or decreased (N^-) are provided at the top of each panel.

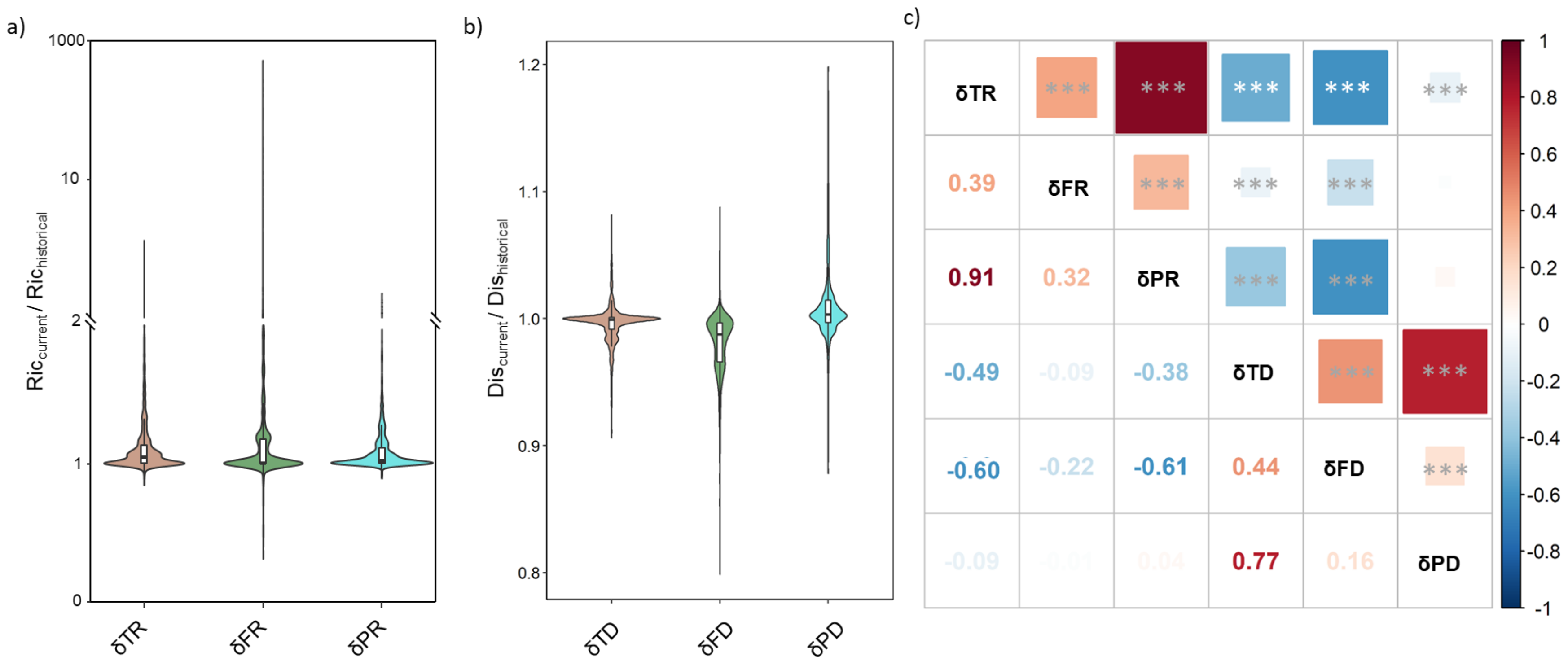


Fig. 4. Changes in biodiversity from historical to current period. a) Violin plots show the distribution of the three richness change indices values. **b)** Violin plots show the distribution of the three dissimilarity change indices values. **c)** Pearson correlation between the changes in diversity indices. (River basin number = 2,456, *** $P < 0.001$)

Supplementary Materials for

Human activities have disrupted freshwater fish biodiversity

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Table S2

Table S3

Materials and methods

Occurrence data: We used the most comprehensive database of freshwater fish species distributions across the world [(*19*) available at http://data.freshwaterbiodiversity.eu]. The fish occurrence database gathers the occurrence of 14,953 species (more than 83% of the freshwater fish species) in 3,119 drainage basins, covering more than 80% of the Earth's surface (*19*). Fish occurrence in each river basin accounts for all the freshwater fish species inhabiting the entire river network of each basin, from 1st order streams to the sea. Each occurrence is paired with a status, either native or non-native established if the species was not historically present in the river basin. Each river basin was assigned to one of the six terrestrial biogeographic realms [i.e., Afrotropical, Australian (including Oceania), Nearctic, Neotropical, Oriental and Palearctic] according to Lévêque et al. (*44*) and Brosse et al. (*45*). Historical fish assemblages composition in the river basins refers to only native species, and thus roughly corresponds to the preindustrial period (i.e., before the 18th century), from when industrialization began and fish introductions for aquaculture, fishing, and ornamental purposes sharply increased (*8, 46, 47*). Similarly, the current sixth mass extinction rises from the beginning of the industrial period (*48*). Therefore, despite a few human mediated species introductions and extinctions occurred before the 18th century (e.g., common carp, *Cyprinus carpio,* introduction in Western Europe), most are more recent. Current fish assemblages composition refers to the non-native species and excludes the local extirpated or extinct native ones. Extirpations refer to the extinction of a fish species within a river basin and data were extracted from the literature reviews of Brosse et al. (*45*) and Diaz et al. (*49*). We then updated these data using IUCN Red lists (*29*). Species with "extinct" or "extinct in the wild" status in the IUCN Red list were thus considered as extinct in their native river basins (Table S2). Although species extirpations/extinctions are probably underestimated for a number of reasons such as the time lag between local report of species extinction and validation of extinction over an entire river basin, we here used the most comprehensive and updated information on fish extinction at the river basin scale.

Functional traits: Among the 14,953 species present in the occurrence database, 10,705 species were morphologically described using pictures and drawings from textbooks and scientific websites. Morphology was assessed using ten traits describing the size and shape of body parts involved in food acquisition and locomotion (*19, 21*). The fish size was described using the maximum body length (Max. Body Length) taken from (*50*). Those maximum body lengths were carefully reviewed, and irrelevant measures have been corrected according to appropriate literature. In addition to size, 11 morphological measures were assessed on side view pictures (Fig. S4a) collected during an extensive literature review including our field data and scientific literature sources made of peer-reviewed articles, books, and scientific websites. We collected at least one picture (photograph or scientific drawing) per species. Only good quality pictures and scientific side view drawings of entire adult animals, with confirmed species identification, were kept. For species with marked sexual dimorphism, we considered male morphology, as female pictures are scarce for most species (especially for Perciformes and Cyprinodontiformes). Intraspecific morphological traits variability was not considered in this study as it hardly affects functional diversity at the large spatial resolution considered (*27*). The nine unitless traits describing the morphology of the fish head (including mouth and eye), body, pectoral and caudal fins (Fig. S4b) were computed as ratios between 11 morphological measures done using ImageJ software (http://rsb.info.nih.gov/ij/index.html). The 10 morphological traits (9 unitless ratios and body size) selected are commonly used in assessment of fish functional diversity [e.g., (*21, 51-53*)] and are linked to the feeding and locomotion functions of fish that themselves determine their contribution to key ecosystem processes such as controlling food webs and nutrient cycles (*4*) (Fig. S4b). The 10 traits were not markedly correlated to each other (Spearman's correlation coefficient, |rho|<0.45 for all the 45 pairwise comparisons). Functional traits not measurable on side pictures, such as gut length, oral gape area and shape, were not included because they are currently only available for a few species in public databases.

Some species have unusual morphologies (species without tails, flatfishes) that prevent from measuring some morphological traits. We thus applied conventions as mentioned in Su et al. (*51*), Toussaint et al. (*21*) and Villéger et al. (*53*) for these few exceptions. Due to the lesion of body parts or the quality of fish pictures, some traits have not been measured for some species. Overall, 24.1% of the values were missing in the raw morphological traits dataset (from 6.9% for maximum body length to 31.4% for relative maxillary length). Those missing values were filled using a phylogenetic generalized linear model (*54, 55*). We then computed a principal component analysis (PCA) using values of the 10 morphological traits for all the species. We selected the first four PCA axes, which explained 68.2% of the total variance among the world's fish functions, to compute the functional diversity indices.

Phylogenetic diversity: Phylogenetic distances between all species were computed on the tree from Rabosky et al. (*56*), including 31,526 marine and freshwater ray-finned fishes. This dataset is based on 11,638 species whose position was estimated from genetic data; the remaining 19,888 species were placed in the tree using stochastic polytomy resolution (*56*).

Environmental and Anthropogenic variables: We selected four environmental and four anthropogenic variables as proxies of the main processes responsible from native biodiversity and impacts of human activities on freshwater ecosystems: (i) NSR: native species richness. (ii) RBA: river basin area; (iii) NPP: net primary productivity; (iv) TEA: temperature anomaly from the Last Glacial Maximum to the present; (v) DOF: degree of fragmentation; (vi) FPT: human footprint; (vii) GDP: gross domestic product; and (viii) USE: consumptive water use. These 8 metrics were overall independent of each other ($|\text{Pearson's } r| < 0.5$), to the exception of NSR and RBA (Fig. S3).

NSR accounts for the biotic resistance hypothesis, which assumes a higher resistance of species rich assemblages against disturbances (*40*). RBA, NPP and TEA were from Tedesco et al. (*19*), and account for the three main hypotheses explaining biodiversity, namely the species-area hypothesis that predicts a positive relationship between river basin area and biodiversity; the species-energy hypothesis that predicts higher biodiversity in energy rich areas, and the historical contingency, which has largely been influenced by the last glacial events in freshwater fish (*57-60*).

FPT is a comprehensive representation of anthropogenic threats to biodiversity, which cumulatively accounts for eight human pressures—built environments, croplands, pasture lands, human population density, night lights, railways, major roadways and navigable waterways (*23*). FPT dataset (resolution: 1 km^2) was taken from Venter et al. (*23*). GDP measures the size of the economy and is defined as the market value of all final goods and services produced within a region in a given period (*61, 62*). GDP dataset (1 square degree resolution) was taken from Nordhaus & Chen (*61*).

DOF accounts for the degree to which river networks are fragmented longitudinally by infrastructure, such as hydropower and irrigation dams (*32*). DOF dataset (resolution: 500 m^2) was taken from Grill et al. (*32*).

USE accounts for water consumption for irrigation, industry, municipal uses and water transfer to other river systems. USE (resolution: 1 km^2) for each river basin was calculated by using $100*(d_{nat}-d_{ant})/d_{nat}$, where d_{nat} represents the total amount of long-term discharge without human influences in each river basin and d_{ant} represents the total amount of average long-term discharge after human extractions and use in each river basin. d_{ant} and d_{nat} were both taken from the WaterGAP model (*32, 63*).

We mapped FTP, GDP, DOF and USE by their relative resolution grid data over the basin-scale map and then calculated the mean value of all the cells covered by each basin. Here we considered the 2,335 river basins (out of the 3,119) with available values for both CCBF (see below) and the eight environmental and anthropogenic variables.

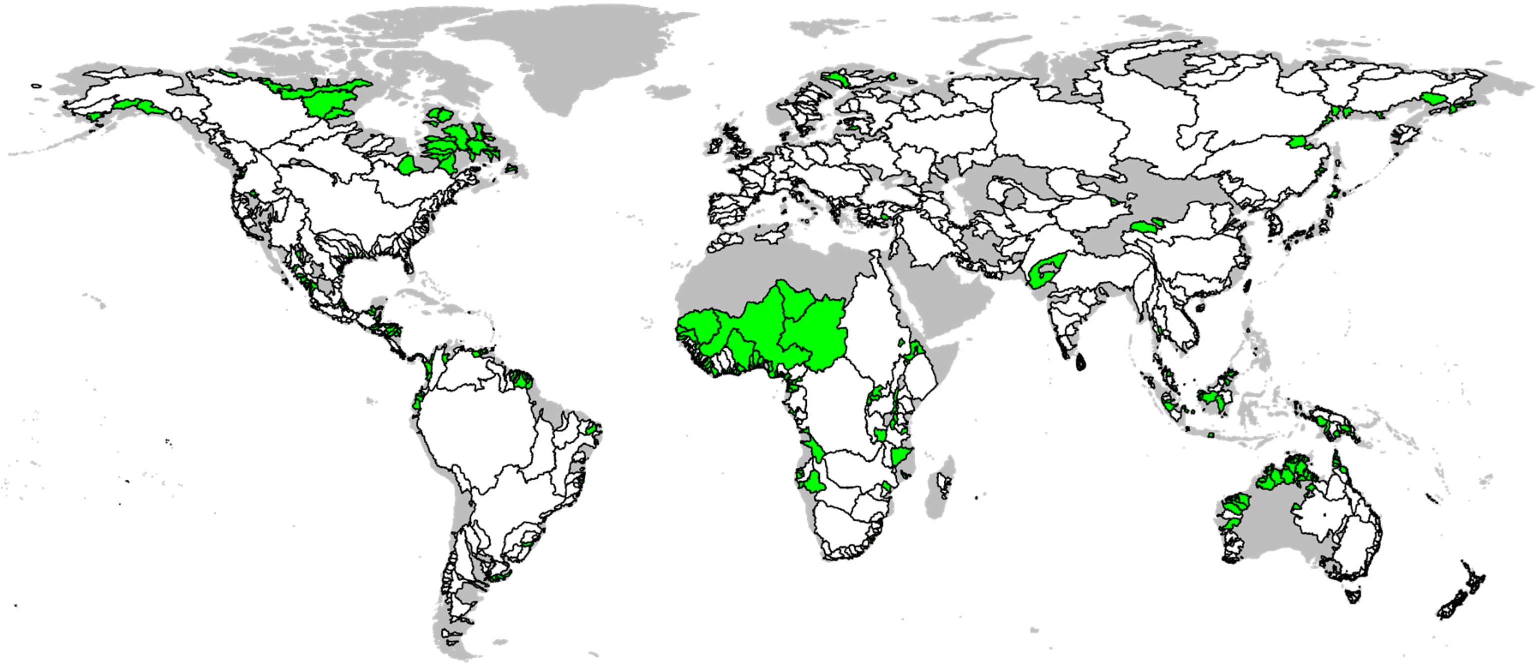
Measuring temporal changes in biodiversity of freshwater fishes: Among the 3,119 river basins with fish occurrence data, diversity indices were measured for all basins with more than 5 fish species to meet the requirements of functional diversity calculation, leading to consider a total of 2,456 river basins. 10,682 species were obtained after matching the occurrence, functional and phylogenetic databases. We assessed the 6 facets of biodiversity (Fig. 1) for fish assemblage inhabiting each of the 2,456 river basins for the current and historical period: taxonomic richness (TR) measured as the number of species, functional richness (FR) measured as the volume of the functional space occupied by an assemblage [i.e., the volume of the minimum convex hull in the functional space which includes all the species in the assemblage, (*64*)], and phylogenetic richness (PR) as the total length of branches linking all species from the assemblage on the phylogenetic tree (*65*). In addition to these indices describing diversity within each assemblage (i.e., alpha-diversity), we also accounted for the dissimilarity among assemblages (i.e., beta-diversity). More specifically, we quantified taxonomic, functional and phylogenetic dissimilarity between each pair of fish assemblages from the same realm as the proportion of total richness in the pair that is not shared by the assemblages, [i.e., Jaccard-index for taxonomic dissimilarity (*66*), beta-FRic for functional dissimilarity (*64*) and UniFrac for phylogenetic dissimilarity (*67*)]. Then the average value of dissimilarity between a fish assemblage and all the other assemblages from the same realm was computed to get for each river basin values of taxonomic dissimilarity (TD), functional dissimilarity (FD), and phylogenetic dissimilarity (PD).

We then calculated for each of these six diversity indices the temporal change (δDI) as the ratio: $DI_{current} / DI_{historical}$. We then computed score for each δDI according to its values: If δDI = 1, it scores 0; if δDI is higher than the median of all the values lower than 1 and lower than the median of all the values higher than 1, it scores 1; and if δDI is lower than the median of all the values lower than 1 or higher than the median of all the values higher than 1, it scores 2. Then we sum up the scores of the six δDI for each basin to get the index of cumulative changes in biodiversity facets which ranges from 0 to 12 (CCBF, Fig. 1).

Thus, our cumulative index accounts for all marked changes in biodiversity facets, not only species loss. Null values are possible only if taxonomic, functional and phylogenetic composition of all assemblages from a realm remained unchanged because otherwise all dissimilarity indices are changed. CCBF scores from 0 to 6 account for moderate changes in biodiversity for all the six facets (all the 6 facets scoring 0 or 1) or strong changes for no more than half of the facets (no more than 3 facets scoring 2). Such CCBF values are considered as moderate changes in biodiversity. CCBF scores from 7 to 12 account for strong changes in biodiversity with all 6 facets changes or more than half of the facets scoring 2. See table S3 for the six diversity indices and CCBF scores for the 2,456 basins.

Statistical analyses: To assess how environmental processes and human activities contributed to the observed change in biodiversity in each realm, we quantified the relative contribution of NSR, RBA, TEA, NPP, FPT, GDP, DOF and USE to the CCBF values of the 2,335 river basins for which all variables were available, using spatial simultaneous autoregressive error models (SAR_{error}). These eight variables were previously scaled to a zero mean and unit variance to ensure equal weighting in the models. We first ran the null model (intercept-only) with none of the variables as a reference. Then we used stepwise regression to select the best models by AIC (Akaike's Information Criterion). We eventually selected the model with the lowest AIC (*68*) (Table S2). We used Nagelkerke's R2 (*69*) as the pseudo R-squared to qualify the final models' performance. After model fitting, we checked for broad spatial autocorrelation in model residuals by computing the Moran's *I* statistic (*70*).

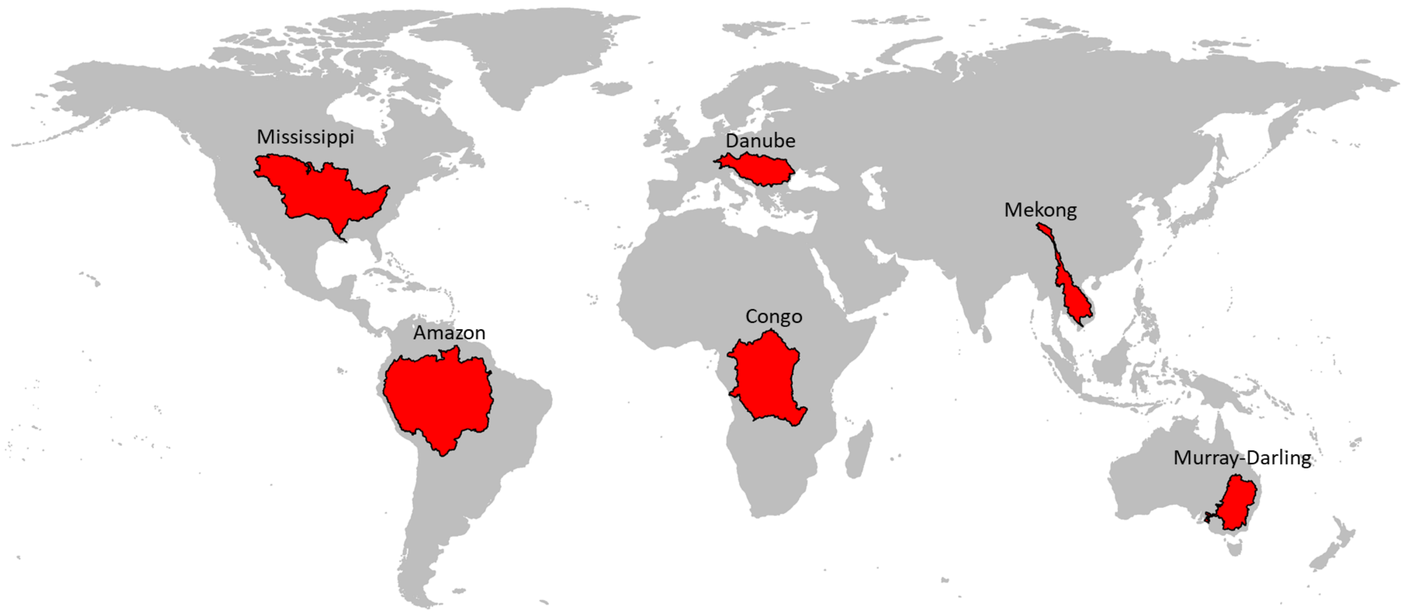
All statistical analyses were performed with the R software environment version 3.3 (*R Core Team*), including the library 'RPhylopars' (*55*) for filling the missing values in the trait database, 'betapart' for computing dissimilarity indices (*71*, *72*), 'spatialreg' and 'spdep' for developing SAR_{error} models (*73*) and performing Moran's *I* tests (*74*).



	Nearctic	Neotropical	Afrotropical	Oriental	Australian	Palearctic	World
Number of basin without changes in richness	76	225	116	97	198	166	878
Percentage of basin number (%)	31.54	60	57.43	28.87	37.08	21.61	35.75
Percentage of basin area (%)	11.45	5.6	34.9	10.06	26.65	1.94	13.4
Percentage of river length (%)	12.77	6.02	34.7	11.15	27.21	2.05	13.42

Fig. S1.

River basins (green color) where the three richness diversity facets remained unchanged from historical to current period.



Basin names	δTR	δFR	δPR	δTD	δFD	δPD	CCBF
Amazon	1.0026	1.0003	1.0036	0.9997	0.9980	0.9991	6
Congo	1.0073	1.0061	1.0122	0.9991	0.9952	0.9989	6
Mekong	1.0346	1.0061	1.0394	0.9977	0.9958	0.9973	6
Danube	1.2247	1.1238	1.1865	0.9797	0.9937	1.0051	9
Mississippi	1.1523	1.0727	1.1863	0.9802	0.9955	0.9885	10
Murray-Darling	1.2642	1.1458	1.2800	0.9906	0.9714	1.0189	11

Fig. S2.

Changes in freshwater fish biodiversity for 6 representative river basins over the world. δTR: taxonomic richness change; δFR: functional richness change; δPR: phylogenetic richness change; δTD: taxonomic dissimilarity change; δFD: functional dissimilarity change; δPD: phylogenetic dissimilarity change. CCBF is the index of cumulative change in biodiversity facets.

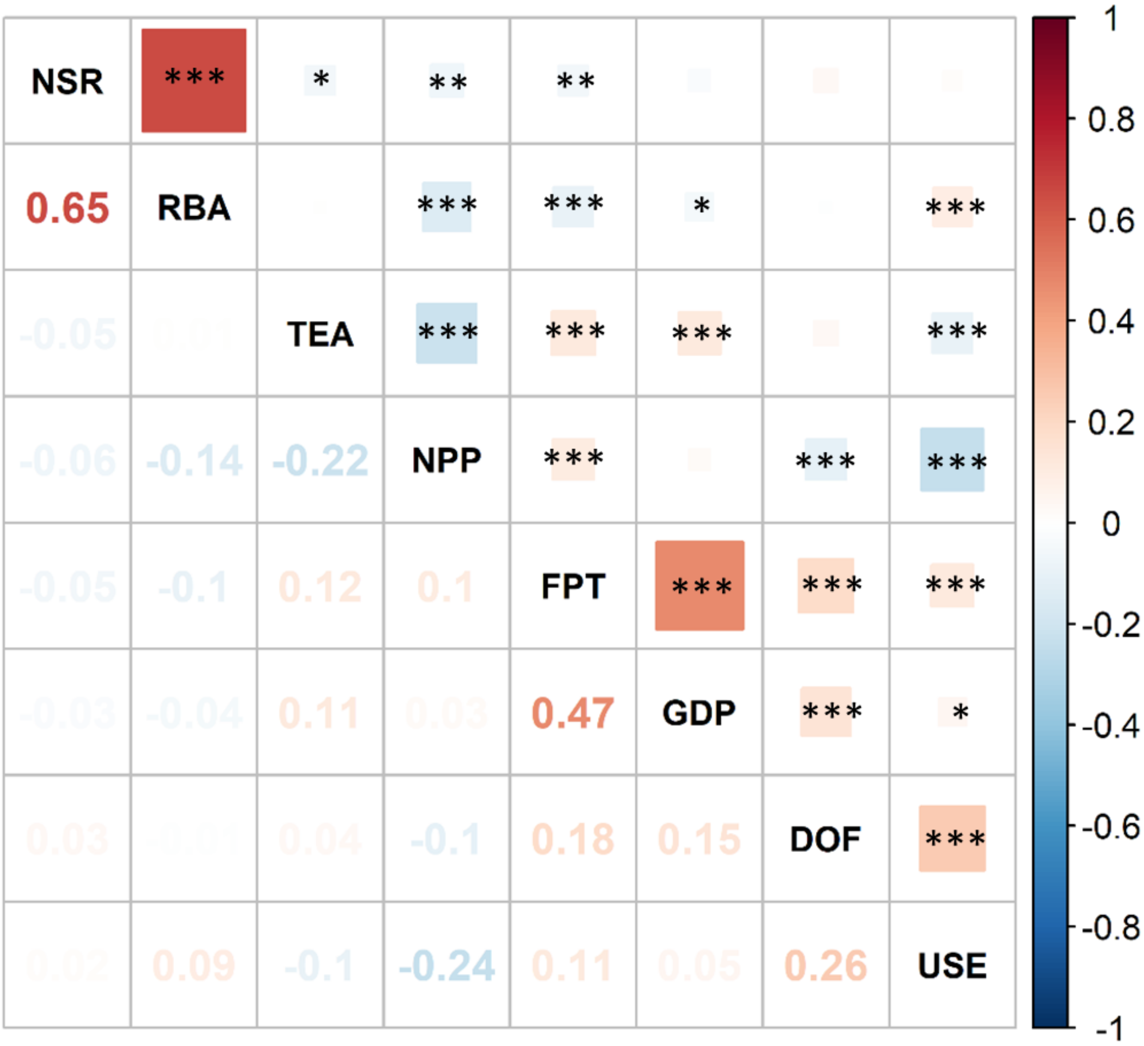
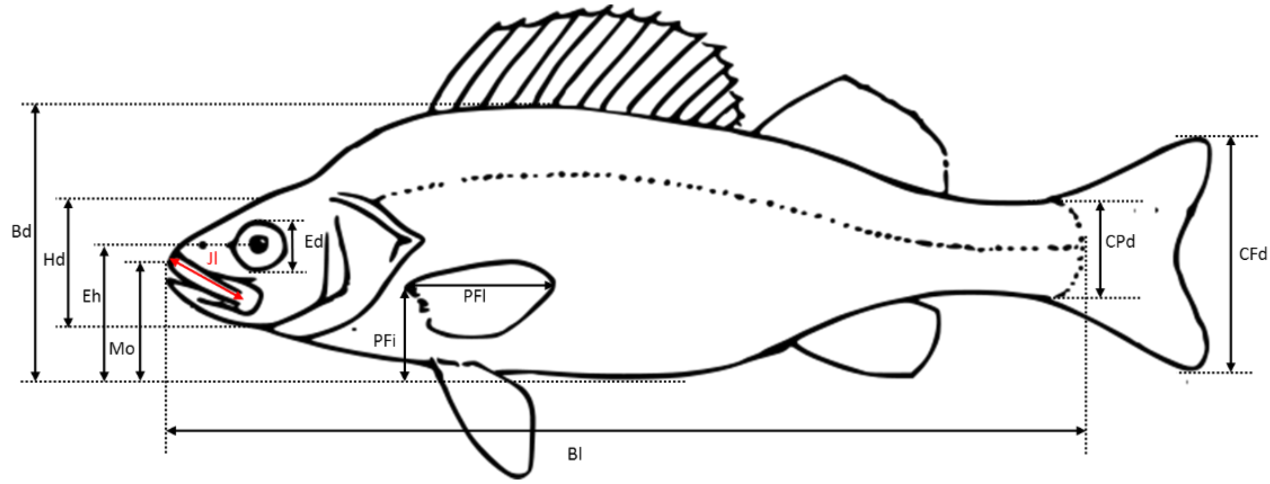


Fig. S3.

Pearson correlation between the eight environmental and human activity variables of the world river basins (n = 2,335). NSR: native species richness; RBA: river basin area; TEA: temperature anomaly since the last glacial maximum; NPP: net primary productivity; FPT: human footprint; GDP: gross domestic product; DOF: degree of fragmentation; USE: consumptive water use. (*** *P* < 0.001, ** *P* < 0.01, * *P* < 0.05)



a. Morphological measurements

Code	Name	Protocol for measurement
Blmax	Maximum Body length	Maximum adult length
Bl	Body length	Standard length (snout to caudal fin basis)
Bd	Body depth	Maximum body depth
Hd	Head depth	Head depth at the vertical of eye
CPd	Caudal peduncle depth	Minimum depth of the caudal peduncle
CFd	Caudal fin depth	Maximum depth of the caudal fin
Ed	Eye diameter	Vertical diameter of the eye
Eh	Eye position	Vertical distance between the centre of the eye to the bottom of the body
Mo	Oral gape position	Vertical distance from the top of the mouth to the bottom of the body
Jl	Maxillary jaw length	Length from snout to the corner of the mouth
PFl	Pectoral fin length	Length of the longest ray of the pectoral fin
PFi	Pectoral fin position	Vertical distance between the upper insertion of the pectoral fin to the bottom of the body

All measurements were made on pictures except Blmax values, which were downloaded from Fishbase.org

b. Morphological traits

Morphological traits	Formula	Potential link with fish functions	References
Maximum body length	BLmax	Size is linked to metabolism, trophic impacts, locomotion ability, nutrient cycling	(*21*)
Body elongation	$\frac{Bl}{Bd}$	Hydrodynamism	(*75*)
Eye vertical position	$\frac{Eh}{Bd}$	Position of fish and/or of its prey in the water column	(*76*)
Relative eye size	$\frac{Ed}{Hd}$	Visual acuity	(*77*)
Oral gape position	$\frac{Mo}{Bd}$	Feeding position in the water column	(*78*, *79*)
Relative maxillary length	$\frac{Jl}{Hd}$	Size of mouth and strength of jaw	(*21*)
Body lateral shape	$\frac{Hd}{Bd}$	Hydrodynamism and head size	(*21*)
Pectoral fin vertical position	$\frac{PFi}{Bd}$	Pectoral fin use for swimming	(*78*)
Pectoral fin size	$\frac{PFl}{Bl}$	Pectoral fin use for swimming	(*80*)
Caudal peduncle throttling	$\frac{CFd}{CPd}$	Caudal propulsion efficiency through reduction of drag	(*81*)

Fig. S4.

Morphological measurements (a) and morphological traits (b) measured on each fish species. For each morphological trait, the potential link with food acquisition and locomotion and associated references are provided.

Table S1.

Results of the spatial simultaneous autoregressive error models (SAR_{error}) showing the coefficients of the selected optimal model in each realm**.** Model with the lowest AIC was selected for each realm. (NSR: native species richness; RBA: river basin area; TEA: temperature anomaly since the last glacial maximum; NPP: net primary productivity; FPT: human footprint; GDP: gross domestic product; DOF: degree of fragmentation; USE: consumptive water use; AIC: Akaike's Information Criterion). The Moran's *I* value represents the remaining autocorrelation on the residuals of the model for the first distance class (i.e., neighbor drainages) in each realm.

Nearctic (n=241)

NULL Model			AIC = 1416.66
Initial Model: NSR+RBA+TEA+NPP+FPT+GDP+DOF+USE			AIC = 1116.66
Optimal Model:NSR+TEA+NPP+FPT+DOF+USE			**AIC = 1113.68**
Statistics in Optimal Model	coefficient (SE)	z-value	*P*
NSR	0.73(0.3)	2.433	**0.015**
TEA	-0.297(0.139)	-2.139	**0.0325**
NPP	0.526(0.297)	1.769	0.0768
FPT	0.482(0.187)	2.581	**0.0099**
DOF	0.722(0.197)	3.667	**0.0002**
USE	0.604(0.196)	3.077	**0.0021**
Nagelkerke's R2	0.353		
Moran's I	-0.006		n.s.

Neotropical (n=350)

NULL Model			AIC = 1578.34
Initial Model: NSR+RBA+TEA+NPP+FPT+GDP+DOF+USE			AIC = 1546.92
Optimal Model: NSR+RBA+TEA+NPP+FPT+GDP+DOF			**AIC = 1544.92**
Statistics in Optimal Model	coefficient (SE)	z-value	*P*
NSR	0.344(0.142)	2.421	**0.0155**
RBA	-0.412(0.168)	-2.45	**0.0143**
TEA	4.54(1.166)	3.893	**0.0001**
NPP	-0.63(0.189)	-3.331	**0.0009**
FPT	0.32(0.189)	1.692	0.0907
GDP	-0.434(0.192)	-2.265	**0.0235**
DOF	0.535(0.203)	2.632	**0.0085**
Nagelkerke's R2	0.336		
Moran's I	-0.03		n.s.

Afrotropical (n=198)

NULL Model			AIC = 831.50
Initial Model: NSR+RBA+TEA+NPP+FPT+GDP+DOF+USE			AIC = 827.53
Optimal Model: NSR+GDP+USE			**AIC = 821.11**
Statistics in Optimal Model	coefficient (SE)	z-value	*P*
NSR	0.247(0.09)	2.749	**0.006**
GDP	3.108(1.598)	1.945	0.0518
USE	0.355(0.127)	2.799	**0.0051**
Nagelkerke's R2	0.444		
Moran's I	-0.044		n.s.

Oriental (n=292)

NULL Model			AIC = 1154.37
Initial Model: NSR+RBA+TEA+NPP+FPT+GDP+DOF+USE			AIC = 1146.19
Optimal Model: FPT+DOF			**AIC = 1137.89**
Statistics in Optimal Model	coefficient (SE)	z-value	*P*
FPT	0.695(0.149)	4.675	**<0.0001**
DOF	0.144(0.083)	1.739	0.082
Nagelkerke's R2	0.246		
Moran's I	-0.003		n.s.

Australian (n=525)

NULL Model			AIC = 2382.61
Initial Model: NSR+RBA+TEA+NPP+FPT+GDP+DOF+USE			AIC = 2361.76
Optimal Model: NSR+RBA+FPT+DOF+USE			**AIC = 2357.49**
Statistics in Optimal Model	coefficient (SE)	z-value	*P*
NSR	1.015(0.474)	2.143	**0.0321**
RBA	1.43(0.328)	4.365	**<0.0001**
FPT	0.4(0.182)	2.194	**0.0282**
DOF	0.208(0.122)	1.701	0.0889
USE	-0.43(0.289)	-1.489	0.1366
Nagelkerke's R2	0.529		
Moran's I	-0.12		n.s.

Palearctic (n=729)

NULL Model			AIC = 3161.83
Initial Model: NSR+RBA+TEA+NPP+FPT+GDP+DOF+USE			AIC = 3101.15
Optimal Model: RBA+TEA+NPP+FPT+GDP+DOF			**AIC = 3097.47**
Statistics in Optimal Model	coefficient (SE)	z-value	*P*
RBA	0.324(0.069)	4.673	**<0.0001**
TEA	-0.356(0.126)	-2.835	**0.0046**
NPP	-0.319(0.181)	-1.761	0.0783
FPT	0.671(0.112)	5.999	**<0.0001**
GDP	-0.155(0.086)	-1.808	0.0706
DOF	0.206(0.063)	3.28	**0.001**
Nagelkerke's R2	0.38		
Moran's I	-0.047		n.s.

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Table S2. (separate file)

Species extirpations/extinctions and introductions in each of the 2456 river basins.

Table S3. (separate file)

The changes in the six diversity indices and the index of cumulative change in biodiversity facets for the fish faunas in 2,456 basins. δTR: change in taxonomic richness; δFR: change in functional richness; δPR: change in phylogenetic richness; δTD: change in taxonomic dissimilarity; δFD: change in functional dissimilarity; δPD: change in phylogenetic dissimilarity; CCBF: index of cumulative change in biodiversity facets.

Tables S2 and S3 are also provided in a public online repository (figshare.com). Here is the private link: https://figshare.com/s/5fadc2c14cbb1f39c25c.